Population structure influences sexual conflict in wild populations of water striders

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Summary

In sexual conflict, aggressive males frequently diminish the long-term reproductive success of females in efforts to gain a short-term advantage over rival males. This short-term advantage can selectively favour high-exploitation males. However, just as the over-exploitation of resources can lead to local extinction, the over-exploitation of females in the form of harassment by aggressive males can yield similar consequences resulting in reduced female fecundity, increased female mortality and overall decline in mating activity. This outcome may often be prevented by selection acting at multiple levels of biological organization. Directional selection favouring aggressive exploitation within groups can be balanced by directional selection amongst groups opposing exploitation. Such between-group selection has recently been demonstrated in laboratory studies of water striders, where the conditional dispersal of individuals increased variation amongst groups and influenced the balance of selection toward reduced male aggression. This multilevel selection (MLS) framework also provides predictive value when investigating natural populations differing in their relative strength of selection within versus among groups. For water striders, the consequences of local exploitation cause fitness differences between groups, favouring less aggressive males. Inconsistently flowing ephemeral streams consist of isolated pools that prevent aggressive male water striders from escaping the consequences of local exploitation. We, therefore, predicted that inconsistently flowing ephemeral streams would favour the evolution of less aggressive males than would perennial streams, which allow aggressive males to move more freely and to escape the group-level costs of their aggression. Comparing two neighbouring streams during the mating season, we found that males dispersed naturally between pools at much higher rates in the perennial stream than in the ephemeral stream. As predicted, we found that males

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from the perennial stream were significantly more aggressive than those from the ephemeral stream. We also found that dispersers were significantly more aggressive than non-dispersers within each stream. These field results illustrate the relevance of the MLS framework in our understanding of the evolution of sexual conflict.

Keywords: multilevel selection, group selection, tragedy of the commons, water strider, sexual conflict, altruism, *Aquarius remigis*.

**Introduction**

Sexual conflict occurs when males and females have separate and conflicting routes to increased fitness. Males frequently diminish the long-term reproductive success of females in an effort to outcompete rivals in the short-term (Chapman et al., 2003). Selection favouring individual self-interest in the form of the overexploitation of a shared resource, such as the overgrazing of a common pasture, can lead to the exhaustion of the resource and detrimental consequences for the group (Hardin, 1968; Rankin et al., 2007). In regards to sexual conflict, overexploitation in the form of the excessive harassment of females by aggressive males can also yield similar consequences resulting in decreased female fecundity, as well as increased female mortality (Bauer et al., 2005; Le Galliard et al., 2005; Rankin & López-Sepulcre, 2005; Sih & Watters, 2005; Rankin & Kokko, 2006; Eldakar et al., 2009a,b). The local advantage of exploitative males makes it difficult to explain how less exploitative — or more prudent — males persist in populations. One potential solution involves selection acting at multiple levels of biological organization (Wilson & Wilson, 2007).

In multi-group populations, the local advantages of exploitation may be countered by selection beyond the local scale (Wilson & Wilson, 2007). If groups vary in the proportion of high-exploitation males, then the differential contribution of groups to the total gene pool can favor prudent males despite their selective disadvantage within each group. This possibility was recently supported in both *Drosophila melanogaster* (Wigby & Chapman, 2005) and the water strider *Aquarius remigis* (Sih & Watters, 2005; Eldakar et al., 2009b) where groups exhibiting less sexual conflict were more productive than higher-conflict groups. Conversely, if the variation between groups was eliminated, selection favoured exploitation based on its local advantage (Eldakar et al., 2009a). Therefore, the balance of these conflicting selection forces is based on the population structure partitioning variance within and